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Are primate folivores ecologically constrained? A comparative analysis of behavioral indicators of within-group feeding competition

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Are primate folivores ecologically constrained? A comparative analysis of behavioral indicators of within-group feeding competition

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Abstract

Are primate folivores ecologically constrained? A comparative analysis of behavioral indicators of within-group feeding competition

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Folivores do not exhibit a direct relationship between group size and daily path length and are consequently believed to experience little feeding competition. However, previous studies lacked sufficient control for ecological variation and did not account for the underlying hierarchical structure inherent in closely related taxa (phylogeny). The present analysis examined daily path length and relative ranging cost in 37 primate species, including 18 folivores, while controlling for ecological variation and phylogeny. Group size effects on group spread, changes in activity budget, and infant to female ratios were similarly investigated as these have been found to indicate feeding competition in folivorous primates. Although relative ranging cost was a not a significant predictor of folivore group size, large groups traveled significantly farther per day, increased group spread per individual, and had lower infant to female ratios than small groups. Large groups spent more time feeding and less time resting than small groups; however, these trends were not significant. A strong phylogenetic signal was detected among species' mean values for average group size ($\lambda = 0.827$). Because primate group size and behavior represent the combination of adapting to present-day environments and phylogenetic inertia, future comparative analyses of feeding competition should account for both current ecological conditions and the phylogenetic signals inherent in the taxa being compared. As suggested by the current study, folivorous primates may utilize a number of foraging strategies, other than increasing daily path length, to alleviate feeding competition. To better assess feeding competition, future research should include alternative correlates of feeding competition such as increased group spread, changes in activity budgets, and decreased female fecundity. The information gained from such research may improve our current interpretations of the 'folivore paradox' and redefine the competitive regime of leaf eating primates.

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INTRODUCTION

Increased feeding competition is generally accepted as an inevitable consequence of group living (Janson and Goldsmith 1995; Koenig 2002; Terbourgh and Janson 1986; Wrangham *et al.* 1993). Therefore, food competition is often used as one of the primary factors in explaining the variation of social structure and group size in social mammals (Alexander 1974; Rubenstein 1986; van Schaik 1989; Wrangham 1980). As group size increases, food patches are depleted more quickly and individuals obtain less food per patch (Chapman and Chapman 2000; Waser 1977). Since groups must travel farther per day to find sufficient food resources for all members, researchers frequently measure the intensity of food competition by the energetic cost of travel (Chapman and Chapman 2000; Janson 1988; Mason 1968; Milton 1984; Wrangham 2000). This model, often referred to as the ecological constraints model, predicts a positive relationship between daily path length and group size. However, the relationship between daily path length and group size is not consistent across dietary guilds (Clutton-Brock and Harvey 1977; Janson and Goldsmith 1995), warranting further investigation into the connection between diet, group size, and daily path length.

The traditional method of comparing daily path length and group size to identify feeding competition in primates has revealed a curious contrast between frugivores and folivores. Frugivorous primates feeding on high-quality, patchily distributed resources, often conform to the predictions of the ecological constraints model, with larger groups traveling farther per day than smaller groups (Chapman 1990; Chapman and Chapman 2000; Chapman *et al.* 1995; van Schaik 1983; Waser 1977; Wrangham *et al.* 1993). Folivorous primates, on the other hand, have shown rather ambiguous relationships between group size and daily path length, with a number of studies finding little to no relationship between these two variables (Clutton-Brock and Harvey 1977; Dias and Strier 2003; Fashing 2001; Struhsaker and Leland 1987; Yeager and Kool 2000).

An alternative metric used to assess feeding competition among primates is relative ranging cost (RRC; Janson and Goldsmith 1995). Instead of relying solely on slope (S) values from the regression between group size and daily path length, RRC

measures the increased ranging cost of an additional group member scaled to the daily path length of a solitary individual (Janson and Goldsmith 1995). Consequently, RRC provides an index of change in relative fitness due to the addition of one more group member (Janson and Goldsmith 1995). In a comparative analysis of group size and RRCs in primates, mean observed group size was significantly and inversely related to RRC values (Janson and Goldsmith 1995). However, as found in most studies on daily path length, this relationship was highly significant for primarily frugivorous species, but not for folivorous species (Janson and Goldsmith 1995).

The absence of a relationship between group size and daily path length, or relative ranging cost, has led researchers to infer that within-group feeding competition is either very weak or inconsequential to folivorous primates, and that folivore group size is not limited by food (Isbell 1991; Isbell and Young 2002; Janson and Goldsmith 1995; Steenbeek and van Schaik 2001; Sterck *et al.* 1997; Wrangham 1980). Theoretically, with little feeding competition, folivores are expected to form relatively large groups to enhance the benefits of group living (e.g., increased predator avoidance [Alexander 1974; Boinski *et al.* 2000; Chapman and Chapman 1996; van Schaik 1983] and improved resource defense [Garber 1988; Wrangham 1980]). However, despite the advantages of larger group sizes, many folivores live in surprisingly small groups compared to frugivores of similar body size (Janson and Goldsmith 1995; Milton 1984; Steenback and van Schaik 2001). This obvious contradiction in group size is referred to as the 'folivore paradox' (Koenig and Borries 2002; Snaith and Chapman 2005; Steenbeek and van Schaik 2001).

Unable to find a strong correlation between group size and ecological conditions in several folivorous primates, a number of researchers have suggested that social factors, such as infanticide risk, limit folivore group size (Chapman and Pavelka 2005; Crockett and Janson 2000; Isbell 1991; Janson and Goldsmith 1995: Steenbeek and van Schaik 2001). Crockett and Janson (2000) offer that as female group size increases, the initial risk of infanticide is greater than the costs of within-group feeding competition. However, as groups become larger, feeding competition may become more costly than infanticide

risk because larger groups are better able to resist group take overs and generate a greater degree of paternity confusion. Consequently, for species already limited by food competition, an increase in group size will generate a higher risk of infanticide, causing females to compete to keep groups small. Although infanticide avoidance may constrain group size in some folivore populations, increasing evidence suggests that ecological factors may also limit folivore group size (Snaith and Chapman 2005, 2007).

Below, I present four lines of evidence to suggest that folivores are food limited and that feeding competition is just as likely to limit group size in folivores as in frugivores (for another review on feeding competition in folivores see Snaith and Chapman 2007): (1) folivores selectively feed on immature leaves, fruits, and flowers, (2) folivores functionally deplete food patches, (3) folivores exhibit subgrouping behavior, and (4) folivores experience reduced foraging efficiency at larger group sizes.

First, contrary to common belief that folivores rely on ubiquitous and evenly distributed food resources, many studies have shown that folivores preferentially select for high-quality young leaves, fruits, and flowers (Chapman and Chapman 2002; Koenig *et al.* 1998; Milton 1980; Oates 1994; Yeager and Kool 2000). Since young leaves generally contain more protein and less fiber than mature leaves, primate folivores likely seek out immature leaves to increase their protein uptake and avoid nitrogen imbalances in the body (Milton 1979; Milton *et al.* 1980). Leaves also vary in nutritional quality and secondary compound content (Glander 1981, 1982). To avoid over-ingestion of secondary compounds and obtain quality nutrients, folivorous primates must feed selectively (Glander 1981, 1982; Milton 1980), often choosing young leaves over more mature leaves and changing ranging patterns to obtain preferred food items from select tree species (Garber and Jelinek 2006; Harris 2006; Hopkins 2011; Milton 1980; Milton 2000).

Second, when assessing food competition among folivores, leaf patches are often assumed to be unable to be depleted (Snaith and Chapman 2005). If leaf patches are boundless, then folivores have no need to increase daily path length to accommodate the faster patch depletion rate of a larger group. Nonetheless, red colobus (*Piliocolobus*

tephrosceles) functionally deplete patches of young leaves, showing decreased intake rates despite increased foraging effort and an inverse relationship between patch occupancy time and both patch size and feeding group size (Snaith and Chapman 2005). Food patch size also limits feeding group size in mantled howler monkeys (Chapman 1988, Leighton and Leighton 1982). Although larger groups are expected to travel farther per day to compensate for faster patch depletion rates, alternative strategies may be employed, such as increased group spread (Arrowood *et al.* 2003; Gillespie and Chapman 2001; Koenig 2000; Saj and Sicotte 2007; Snaith and Chapman 2008; Teichrob 2009). As groups become larger an increase in group spread mediates the effects of communal depletion by placing fewer individuals per feeding patch (Leighton and Leighton 1982). Moreover, in four groups of black howlers (*Alouatta pigra*) group spread explained at least 24 percent of the variation in daily path length (Arrowood *et al*. 2003).

Third, a number of studies have demonstrated that some folivorous primates exhibit subgrouping behavior, with large groups temporarily dividing into smaller foraging groups that vary in size and composition (Bezanson *et al.* 2008; Chapman and Chapman 2000; Jones 1995; Leighton and Leighton 1982; Oates 1994; Snaith and Chapman 2008; Struhsaker *et al.* 2004; Yeager and Kool 2000). Temporary variation in group size is well documented in frugivores (fission-fusion) as a response to changing ecological conditions (Chapman 1990; Nishida 1968; Symington 1990; van Schaik 1999; Wrangham *et al.* 1996), and folivores may practice subgrouping behavior to reduce within-group scramble competition when resources become scarce. In fact, mantled howler monkeys inhabiting a seasonal moist tropical forest in Panama spend significantly more time in subgroups during the dry season, when food resources become limited (Hopkins and Ellis, unpublished data).

Finally, changes in group activity budgets and/or female fecundity and infant survival rates may be indicative of feeding competition and reduced foraging efficiency in folivores. For example, reduced foraging efficiency may be identified by increased feeding and/or travel time, compensated by decreased resting and/or social time (Altmann 1980; Caraco 1979; Dunbar and Dunbar 1988). In two groups of red colobus, the larger

group traveled significantly more and rested significantly less than the small group (Gillespie and Chapman 2001). Similarly, in two groups of ursine colobus (*Colobus vellerosus*), the adult females of the large group spent significantly more time feeding than the adult females of the small group (Saj and Sicotte 2007). As feeding competition increases, female reproductive success may be compromised (Dunbar 1988; van Schaik 1983). Analyzing birthrate and group size, van Schaik (1983) found that birth rate decreased as group size increased, and that this relationship was more pronounced in folivores than frugivores. In red colobus, female reproductive success declines as the number of females in the group increases (Snaith and Chapman 2008). Furthermore, in Phayre's leaf monkeys (*Trachypithecus phayrei*) infants in larger groups develop more slowly, are weaned later, and females reproduce at a slower pace (Borries *et al.* 2008).

The evidence outlined above suggests that primate folivores do experience within-group feeding competition and that folivore group size may be ecologically constrained. Yet, some folivore groups fail to fit the predictions of the ecological constraints model of larger groups traveling farther per day than smaller groups. Further investigation into primate diet, group size, and daily path length is needed to reconcile the conflicting descriptions of feeding competition in folivorous primates.

Previous studies assessing the relationship between primate group size and daily path length may have been limited in several ways. First, studies that were unable to find a correlation between folivore daily path length and group size (Clutton-Brock and Harvey 1977; Dias and Strier 2003; Fashing 2001; Struhsaker and Leland 1987; Yeager and Kool 2000) may have lacked sufficient ecological controls. Comparing data from different time periods, across different habitats, or between different species, can lead to inaccurate conclusions about group size and daily travel (Janson 1988; Snaith and Chapman 2007). In more recent analyses of folivore daily path length, researchers, aiming to control for ecological variation, found that daily path length does increase with group size in folivorous primates including, but not limited to *Alouatta palliata* (Hopkins 2011; Stoner 1996), *Presbytis thomasi* (Steenbeek and van Schaik 2001), and *Gorilla beringei* (Ganas and Robbins 2005). Second, previous comparative studies may have

lacked sufficient phylogenetic controls (Koenig 2002; Snaith and Chapman 2007). Because behavior, morphology, physiology, and life history patterns are heritable, variation in these patterns are greater between taxonomic groups than within taxonomic groups. Integrating phylogenetic relationships into comparative analyses allows researchers to rectify the non-independence of data due to taxonomic clustering (Felsenstein 1985). Third, variation in sampling efforts may have led to an overrepresentation of some species compared to others. An unbalanced number of studies per species can result in coefficients that are biased towards the species with the greatest number of samples. Fourth, previous studies may not have accounted for predation risk. If group size is a balance between social foraging costs and individual predation risk (Dunbar 1988; Janson and Goldsmith 1995; Terbogh and Janson 1986; van Schaik 1983), then group size may vary in relation to factors that influence predation risk such as body size (Cheney and Wrangham 1987) and terrestriality (Crook and Gartlan 1966). Fifth, female philopatry may lead to different mechanisms of food competition where larger groups gain a foraging advantage over smaller groups (Janson and Goldsmith 1980; Wrangham 1980). Therefore, recognizing primate species as female dispersing or non-female dispersing may alter final conclusions about optimum group size. Finally, as shown above, primates may use behavioral tactics other than increasing daily path length to reduce feeding competition such as increasing group spread or regulating daily activity budgets. These behaviors are rarely examined across primate taxa and may prove to be better indicators of feeding competition in folivores than daily path length.

The aim of the current study was twofold. First, improve upon previous analyses of daily path length and relative ranging costs in primates by increasing the number of folivorous species examined, controlling for phylogeny, ecological variation, predation risk, and social factors (e.g. female dispersal and infanticide risk). Second, test for alternative indicators of feeding competition in primate folivores, such as decreased fecundity, increased group spread, and changes to activity budgets in larger groups. If daily path length and group size are found to be highly correlated in primate folivores, then a relatively simple model between daily path length and group size may still be

appropriate for assessing feeding competition in folivores. However, if the relationship between daily path length and group size remains ambiguous, yet fecundity, group spread, and changes to activity budgets reveal strong relationships with increasing group size, a more complex model incorporating these behaviors is called for to better assess feeding competition in folivorous primates.

HYPOTHESES AND PREDICTIONS (TABLE 1)

Hypothesis 1: Relative ranging cost constrains group size in frugivorous AND folivorous primates.

Therefore, I predicted:

1.1) An inverse relationship between relative ranging cost and group size in both frugivorous and folivorous species.

1.2) An inverse relationship between slope (S) values and group size.

Hypothesis 2: Group size generates energetic and reproductive costs in frugivorous AND folivorous primates.

Therefore, I predicted:

2.1) A positive relationship between group size and daily path length in both frugivores and folivores.

2.2) An inverse relationship between group size and infant to female ratios (proxy for female fecundity).

2.3) An inverse relationship between group size and presence of infanticide within a species.

Hypothesis 3: Folivorous primates utilize alternative strategies, in addition to increasing daily path length, to mediate within-group feeding competition.

Therefore, I predicted:

3.1) Increased group spread per individual in larger groups than smaller groups.

3.2) An inverse relationship between group spread and daily path length.

3.3) A positive relationship between group size and time spent feeding and traveling, with an inverse relationship between group size and time spent resting.

Hypothesis 4: Immature leaves are a patchy resource, thus, folivorous primates have daily path lengths that correlate to the amount of immature leaves in the diet.

Therefore, I predicted:

4.1) A positive relationship between daily path length and the percent of immature leaves in the diet.

METHODS

DATA COLLECTION

To obtain information on the behavior, ecology, and morphology of different primate species, I reviewed primatological literature using the PrimateLit database (available online at http://primatelit.library.wisc.edu), the ProQuest Full Text Dissertation and Theses database available through the University of Texas at Austin, and various books on primatology (Appendix I). To be included in analyses studies had to provide daily path lengths for at least two groups of different sizes studied at the same site simultaneously. Study populations also had to forage exclusively on natural resources.

In all, I acquired data from 49 studies, covering 37 species (19 frugivores, 18 folivores) and 21 genera (Appendix I). Prior to analyses, five of these studies were split into two separate datasets because the data either a) came from two different time periods (Saj and Sicotte 2007); b) came from two different localities (Gomez-Posada *et al.* 2007; Siex 2003; Struhsaker 2010); or c) contained data for two different species (Agostini *et al.* 2010). This gave me a total of 54 studies (20 frugivore, 34 folivore) with which to run analyses. Several differences exist between the dataset used here and that used by Janson and Goldsmith (1995). First, five studies used in the Janson and Goldsmith (1995) analysis were removed because within population data were not collected during the same time period or from the same locality. These studies included three frugivores (*Callicebus torquatus* (Kinzey 1981); *Papio hamadryas* (Sigg and Stolba 1981); *Macaca fuscata* (Ikeda 1982) and two folivores (*Theropithecus gelada* (Iwamoto and Dunbar 1983); *Colobus badius* (Struhsaker and Leland 1987). Second, two study populations used by Janson and Goldsmith (1995) were reduced to two groups because data were not collected on all groups during same the time period or from the same locality. These studies included a frugivorous species (*Cercopithecus ascanius*; Struhsaker and Leland 1987) and a folivorous species (*Alouatta palliata*; Chivers 1969). In all, the current dataset triples the number of folivorous species used in analyses from the original Janson and Goldsmith (1995) study on relative ranging cost.

Daily path length was recorded as distance traveled in a day (no less than 8 hours of continuous observation) and measured as the straight line distance of mean group location at time intervals of 30 minutes or less. When cited, group spread was recorded as the mean diameter (m) of the group. Activity budgets were based on the percent of scans spent feeding, traveling, and/or resting. Primates were classified as frugivores or folivores based on the percentage of total leaves in the diet. Following earlier studies (Janson and Goldsmith 1995; Majola *et al.* 2008), a primate was considered a folivore if more than 40% of its diet consisted of leaves. Dietary categories were not differentiated any further. Hence, I did not consider if primarily frugivorous primates complimented their diet with insects or with leaves, although these details may impact ranging patterns (Janson 1988). In species exhibiting multi-level societies, such as spider monkeys (*Ateles*), only the foraging group size was considered.

A proxy of female fecundity was estimated using the ratio of the number of infants to the number of adult females in each group (Majola *et al.* 2008; van Schaik 1983). Terrestriality and female body size were collected as proxies for predation risk as terrestrial and/or small bodied primates are at higher risk of predation than arboreal and/or large bodied primates (Cheney and Wrangham 1987; Crook and Gartlan 1996; Janson and Goldsmith 1995). Species were classified as female dispersing (including species with bisexual dispersal) or non-female dispersing. Average annual rainfall (mm) was collected for each study site as a proxy for habitat productivity. In all analyses group size, daily path length, and body size were log-transformed to reach normality. Significance levels were Bonferroni corrected (i.e. original probability value divided by the number of comparisons in the sample) to account for the increasing probability of finding a significant result by chance alone as the number of comparisons increased.

ANALYSES

Tests of Hypothesis 1: Relative ranging cost constrains primate group size in frugivorous AND folivorous primates.

To find RRC values a regression slope (S) was fitted between group size and daily path length for each study population (Figure 1; Janson and Goldsmith 1995). Following

Janson and Goldsmith (1995), the expected foraging effort of a solitary animal (H) was then estimated in meters using the formula:

H = slope (meters/individual) · 1 (individual) + intercept (meters) (*Equation 1*)

From this, RRC was calculated as:

RRC = slope (S)/H (*Equation 2*)

and measured in units of solitary daily path length per added group member (Janson and Goldsmith 1995).

Three analyses were used to investigate the relationship between group size and relative ranging cost (RRC): ordinary least squares regression (OLS), phylogenetic generalized least squares regression (PGLS), and linear mixed effects modeling (LMM). RRC and S values were further compared between frugivorous and folivorous primates using a Wilcoxon Rank Sum Test.

OLS

To allow direct comparison between the original study of relative ranging costs (Janson and Goldsmith 1995) and the present expanded dataset (Appendix I), I used an OLS regression between RRC, diet category, and average group size. Relative ranging cost was set as the dependent variable whereas diet category and average group size were set as the independent variables. Despite having high S values, two *Alouatta* populations (Hopkins 2008; Stoner 1996) were excluded from analyses because they exhibited negative intercepts. Using negative intercepts to find RRC would automatically result in a negative RRC value, indicating that as groups get larger less travel is needed to satisfy daily nutritional demands, when in fact, the opposite relationship is characteristic of these populations.

PGLS

Although the OLS regression allowed the results of the current study to be directly compared to those of Janson and Goldsmith (1995), this type of regression does not account for phylogeny or sample inflation (more groups of one species sampled than others). To test if group size was phylogenetically constrained among taxa, I used

phylogenetic generalized least squares regression (PGLS). PGLS regression assumes that residual variation among species is correlated, with the correlation given by a process of Brownian motion evolution along a phylogenetic tree. A trait that is independent of phylogeny is indicated by a value of $\lambda = 0$, whereas a trait evolving in correlation to the given phylogeny is indicated by a value of $\lambda = 1$. Values of λ that are not significantly close to 0 or 1, would indicate that traits have evolved according to a process in which the effect of phylogeny is weaker than expected by a Brownian model of evolution (Freckleton *et al.* 2002). In general, PGLS methods assume a sample size of 1, therefore, all population values were averaged to provide mean values for each species. Although some authors have suggested representing within species variation by adding branch lengths of 0 to a species tip (Felsenstein 2008; Ives *et al.* 2007), debate over the validity of this approach exists (Garamszegi and Moller 2010; C. Nunn, personal communication).

The phylogenetic tree topology used in PGLS analyses was summarized and constructed using a 50% majority rule consensus tree obtained from 10KTrees Primates: Version 3 (Figure 2; Arnold 2010). At present, 10KTrees does not contain *Presbytis thomasi* within its database, therefore, *P. comata* was substituted for *P. thomasi.* This had no effect on phylogenetic relationships within the tree since *P. comata* and *P. thomasi* have the same divergence time from *Semnopithecus entellus* (Meyer *et al.* 2011). Phylogenetic relationships have not been confirmed for *Chlorocebus djamdjamensis*, therefore, this taxon was omitted from PGLS analyses.

LMM

A linear mixed effects model (LMM) was employed to alleviate potential statistical errors stemming from an unbalanced number of study populations per species and non-independence of closely related taxa. For the initial model, RRC, diet, female body size, terrestriality, female dispersal, and rainfall were set as fixed factors (Table 2) and species nested within genus, nested within family, was set as a random factor to account for phylogenetic constraints.

Tests of Hypothesis 2: Group size generates energetic and reproductive costs in frugivorous AND folivorous primates.

I used cross-classified random effects models (CCMM) to analyze the effects of group size on daily path length and group size on infant to female ratios. CCMMs acknowledge that data may be structured under two cross-cutting hierarchies (Goldstein 2011), which in this case would be groups within a study population and taxonomy. To account for this underlying data structure, study and species nested within genus, nested within family, were set as crossed random factors with group size, diet, female body size, terrestriality, female dispersal, and rainfall set as fixed factors. Only 29 of the 54 studies contained enough demographic data to derive infant to female ratios. These studies included 22 (11 species) folivore populations and 7 (5 species) frugivore populations.

Cross-classified random effects models were similarly utilized to assess whether frugivorous and folivorous species with infanticide had smaller group sizes than species without infanticide. Diet and presence of infanticide were set as fixed factors with study and species nested within genus, nested within family, set as crossed random factors. The proportion of frugivorous and folivorous species reported to have infanticide were further compared using a chi-square test for goodness of fit to investigate if folivores have significantly higher occurrences of infanticide than frugivores.

Tests of Hypothesis 3: Folivorous primates utilize alternative strategies, in addition to increasing daily path length, to mediate within-group feeding competition.

No more than seven studies contained enough data to test the effects of increasing group size on group spread and activity budgets. Therefore, linear mixed effects models were employed on a subset of the overall data (Appendix II). For each dependent variable (group spread, time spent feeding, time spent traveling, and time spent resting), group size was set as a fixed factor and species nested within genus, nested within family, was set as a random factor.

Tests of Hypothesis 4: Immature leaves are a patchy resource, thus, folivorous primates have daily path lengths that correlate to the amount of immature leaves in the diet.

A linear mixed effects model was used to test if daily path length was affected by the percent of time spent feeding on immature leaves. For this model, daily path length was set as the dependent variable, percent of immature leaves in diet and group size were set as the fixed factors, and species nested within genus, nested within family, was set as a random factor.

MODEL SELECTION

All statistical analyses were executed in R version 2.12.2 (2011). Phylogenetic generalized least squares, linear mixed effects models, and cross-classified models were selected using the R packages *caper* (Orme *et al.* 2011), *APE* (Paradis *et al.* 2011), *lme4* (Bates *et al.* 2011) and *LMERConvenienceFunctions* (Tremblay, 2011). For each response variable, I ran the fullest model possible, accepting all biologically meaningful interactions between explanatory variables (Whittingham *et al.* 2006). Next the full model was backfit on t-values with log likelihood ratio tests using the *LMERConvenienceFunctions* package. The model with the lowest Akaike's Information Criterion (AIC) for each response variable was chosen and *p*-values were calculated for each explanatory variable and interaction from the *t* statistic.

RESULTS

Group size and relative ranging cost

OLS

As predicted, mean primate group size decreased as RRC increased. The inverse relationship between RRC and mean group size was significant (N = 52, $r^2 = 0.173$, $p < 0.01$) for the dataset combining frugivores and folivores. However, when folivores and frugivores were analyzed separately, the relationship was only significant for frugivores (Figure 3).

PGLS

A phylogenetic signal was detected in the PGLS regression of species' mean values for RRC on average group size ($\lambda = 0.827$). However, this value is significantly different from 1 ($p < 0.02$), indicating that group size has not evolved according to a process expected under a Brownian model of evolution (Freckleton *et al.* 2002). As in the OLS model, RRC remained a significant predictor of average group size for frugivores, but not folivores (Figure 4). When comparing the two models, the PGLS model had a smaller AIC value, but a lower correlation value (OLS: N = 34, $r^2 = 0.307$, $p < 0.001$, $AIC = 68.7$; PGLS: N = 34, $r^2 = 0.218$, $p < 0.001$, $AIC = 61.7$).

Due to the phylogenetic signal detected in PGLS analyses, an a posteriori investigation was conducted on average group size between families of leaf eating primates using a Kruskal-Wallis test. Significant differences in average group size were discovered (H = 16.95, df = 3, $p < 0.001$). Leaf eating cercopithecioids live in much larger groups than leaf eating atelids, and leaf eating indriids reside in smaller groups than either cercopithecoids or atelids. No significant difference was found in RRC values among these groups (H = 4.84, df = 3, $p = 0.184$).

LMM

When accounting for phylogeny and sample inflation, among the fixed factors (RRC, diet, female body size, terrestriality, female dispersal and territoriality), only RRC and its interaction with diet were significant predictors of group size (Table 4). Larger RRC

values resulted in smaller group sizes. Similar to the results of the OLS and PGLS regressions, the inverse relationship between RRC and group size was only significant for frugivores.

When RRC values were compared between frugivores and folivores using a Wilcoxon rank sum test, no significant difference was detected between the two groups (W=419, $p = 0.160$). Slope (S) values of the regression between group size and daily path length, on the other hand, were significantly different between the two diet types (W = 449, $p < 0.01$), with frugivores having much larger slopes than folivores (Figure 5).

Group size, daily path length, and female fecundity

CCMM

Daily path length was significantly related to group size, diet, and the interaction between group size and diet (Table 5). Female body size, terrestriality, female dispersal, and rainfall, on the other hand, had non-significant effects on daily path length. Daily path length significantly increased as group size increased in both diet types. However, folivores, exhibited shorter daily path lengths than frugivores.

Group size had a significant inverse relationship to the ratio of infants to females (Table 6). Body size did not have a main effect on the ratio of infants to females. However, a significant interaction between body size and terrestriality on infant to female ratios was discovered. Female dispersal also had a significant effect on infant to female ratios, with female biased or mixed sex dispersal having higher infant to female ratios. In contrast, the significant interaction between female dispersal and diet resulted in a reduced number of infants per female. Finally, average annual rainfall had a significant negative relationship on infant to female ratios.

No relationship existed between group size and the presence of infanticide within frugivorous or folivorous species (Table 7). Furthermore, the proportion of folivores (81%) reported to have infanticide was no greater than the proportion of frugivores (69%) reported to have infanticide (N = 35, $\chi^2 = 0.174$, $df = 1$, $p = 0.676$).

Group size, group spread, activity budgets, and percent of immature leaves in the diet
LMM

Of the 54 studies containing daily path length for at least two groups of different sizes, 7 studies (5 species) reported group spread, 6 studies (6 species) contained activity budgets, and 7 studies (5 species) reported diet data (Appendix II). Group spread per individual (m) significantly increased with group size (N = 26, df = 24, $p < 0.001$). However, no relationship was found between group spread and daily path length (N = 26, df = 24, $p = 0.86$). Although larger groups spent more time feeding and less time resting than smaller groups, these relationships were not significant, after applying Bonferroni corrections (N = 20, df = 18, $p = 0.24$ and N = 18, df = 16, $p = 0.024$, respectively). Larger groups did, however, spend significantly more time feeding on immature leaves than smaller groups (N = 20, df = 18, $p < 0.01$). Nonetheless, no relationship was found between time spent feeding on immature leaves and daily path length (N = 20, df = 18, $p = 0.38$). Finally, no relationship was identified between group size and time spent traveling (N = 18, df = 16, $p = 0.92$).

DISCUSSION

The folivore paradox is based on the assumption that all folivorous primates have little to no within-group feeding competition, and thus should live in relatively large groups to avoid predators and/or infanticide (Treves and Chapman 1996; Koenig and Borries 2002; Snaith and Chapman 2005; Steenbeek and can Schaik 2001). However, the basis of this notion emanated from previous studies that generally lacked sufficient control for ecological variation and/or made comparisons between groups during different time periods or from different habitats. The current comparative study improved upon previous analyses of daily path length and relative ranging cost in primates by tripling the number of folivorous species investigated, while controlling for phylogeny and ecological variation. I also investigated the effects of group size on group spread, changes in activity budget, and infant to female ratios as these have been suggested to be possible indicators of within-group feeding competition in folivores (Arrowood *et al.* 2003; Gillespie and Chapman 2001; Saj and Sicotte 2007; Snaith and Chapman 2008; Teichrob 2009; van Schaik 1983). Although RRC remained a non-significant predictor of folivore group size, folivores in larger groups were found to travel farther per day, spend more time feeding, and less time resting. Average group spread per individual increased as group size increased. Furthermore, larger groups had lower infant to female ratios than smaller groups. If folivorous primates suffer negative consequences at larger group sizes, as these findings suggest, then folivore group size may be ecologically constrained.

Group size and relative ranging cost

Despite an expanded dataset from that used by Janson and Goldsmith (1995), relative ranging cost (RRC) was not a significant predictor of folivore group size. The absence of a relationship between RRC and folivore group size may invoke conclusions that folivores do not experience within-group scramble competition over food resources (Clutton-Brock and Harvey 1977; Dias and Strier 2003; Fashing 2001; Janson and Goldsmith 1995; Struhsaker and Leland 1987; Yeager and Kool 2000). Nevertheless, folivore RRC values are statistically indistinguishable from frugivore RRC values. This result is not necessarily intuitive, as slope (S) values between the two diet types are

significantly different, with folivores having smaller S values than frugivores. One reason that RRC values may be similar between frugivores and folivores despite large differences in S values is that folivores also have comparatively low intercept (H) values (Janson and Goldsmith 1995), a likely result of shorter daily path lengths (discussed below). More importantly, the inherent calculation of RRC (S/H) forces researchers to exclude populations with negative intercept (H) values, despite large slope (S) values. Such a method may have tremendous impacts on final interpretations of feeding competition in primates since it often results in the removal of folivore populations with the strongest signal (largest slope values). Consequently, RRC may not be the most statistically sound metric to use in comparative analyses of feeding competition.

The failure of slope (S), or RRC, to predict large group sizes in folivorous primates, may indicate that folivores are experiencing some type of constraint on group size other than feeding competition. In both models accounting for non-independence of closely related taxa (PGLS, LMM), group size was heavily influenced by phylogeny. Variation in primate social structure is similarly characterized by a strong phylogenetic signal (DiFiore and Rendall 1994; Chan 1996; Matsumara 1999; Thierry *et al.* 2000, 2008). Because phylogenetic signals can be due to either constant ecological conditions or evolutionary constraints (Balasubramania *et al.* 2012), primate group size and social structure likely represent the combination of adapting to the present-day environment and phylogenetic inertia (Struhsaker 1969; Terborgh and Janson 1986; DiFiore and Rendall; Thierry et al 2000, 2008; Korstjens and Dunbar 2002). Utilizing phylogeny as the null hypothesis in comparative analyses may allow primatologists to better differentiate which behaviors are the result of socioecology versus the relics of evolutionary history.

Group size, daily path length, and female fecundity

Although frugivores were found to have longer average daily path lengths than folivores, primates of both diet types presented significant positive relationships with group size. These results match the predictions of the ecological constraints model (Chapman and Chapman 2000; Janson 1988; Mason 1968; Milton 1984; Wrangham 2000): larger groups need to travel farther per day than smaller groups to compensate for faster depletion rates

per unit area. When food is reduced below a critical level, and individuals no longer receive an energetic benefit from remaining in the area, individuals/groups usually have two options: 1) move to the first available food source, even if it is of poorer quality, opposed to traveling farther to the next high quality food source, or 2) utilize a 'high cost–high yield' strategy in which individuals/groups will travel farther, passing lower quality food sources, to reach higher quality food sources (Harrison 1985, Janson 1988). Such a large discrepancy in frugivore and folivore daily path lengths may occur because frugivores are able to utilize the second strategy at little to no cost, whereas folivores, already metabolically constrained (Milton 1980), are unable to gamble on reaching the next high quality resource.

Both frugivores and folivores experienced lower infant to female ratios at larger group sizes. With female fecundity a direct consequence of physical state, or ability to meet daily nutritional demands, this result suggests that greater foraging effort experienced by larger groups can have negative impacts on individual fitness (Dunbar 1988, van Schaik 1983; Whitten 1983). Contra previous findings on diet and female fecundity (van Schaik 1983), folivores had higher infant to female ratios than frugivores. This difference may be due to the smaller sample size of frugivores to folivores. Another explanation may be the consequence of fewer folivorous species exhibiting female philopatry (in this study). Species with female philopatry tend to demonstrate greater within-group contest competition and strict dominance hierarchies (Sterck et al. 1997). Dominance hierarchies allow for individuals to have differential access to resources which may translate to larger differentiations in reproduction rates (Janson and van Schaik 1988; Koenig 2002; Lomnicki 1988; van Schaik, 1989), and/or infant survival rates compared to females in groups with female dispersal.

Infant to female ratios were also significantly impacted by terrestriality and average annual rainfall. Terrestrial species were associated with higher female fecundity rates than arboreal species. However, this result may be biased by the small sample of terrestrial species, as well as the fact that two of the three terrestrial species used in analyses were great apes (*Gorilla beringei* and *Pan troglodytes verus*). Study populations

with higher average annual rainfall had decreased infant to female ratios. According to Semple and collaborators (2002), primates living in wetter habitats have increased concentrations of lymphocytes and phagocytes, with the latter primarily involved in micro-organism and macro-parasitic infection. High parasite loads may lead to lower female fitness and lower infant survival in some populations (Nunn and Altizer 2006). Moreover, plant productivity has been shown to decrease at levels of rainfall over 2,500 mm (likely caused by soil leaching and reduced amounts of solar radiation; Kay *et al.* 1997). If higher rainfall limits plant production, females may have a harder time meeting nutritional demands, resulting in lower female reproductive rates and/or fecundity.

Many authors argue that folivore group size is heavily influenced by male to male intolerance and infanticide risk (Crockett and Janson 2000; Isbell 1991; Janson and Goldsmith 1995; Steenback and van Schaik 2001). If groups are remaining small in size to reduce the risk of male takeovers (Crockett and Janson 2000) opposed to ecological constraints then ranging behavior is not expected to correlate with group size. However, in the current dataset species with infanticide did not have smaller group sizes, nor was the proportion of folivores reported to have infanticide greater than the proportion of frugivores reported to have infanticide. These findings suggest that infanticide alone cannot solely explain constraints on group size for all folivorous species. Furthermore, primates may counteract infanticide in different ways. As previously stated, the initial risk of infanticide may be greater than the costs of within-group feeding competition at smaller group sizes. However, as groups become larger, feeding competition becomes more costly than infanticide risk because larger groups are better able to resist group take overs and generate a greater degree of paternity confusion (Crockett and Janson 2000). If this is the case, then some folivore populations may increase group size to prevent male takeovers and infanticide. This counterstrategy has been witnessed in largely folivorous species such as Hanuman langurs (*Semnopithecus entellus*, Treves and Chapman 1996). More data concerning the rate of infanticide as well as counterstrategies among and within species are needed to better understand how infanticide risk influences primate group size.

Group size, group spread, activity budgets, and percent of immature leaves in the diet

Group spread may be one way to mediate the effects of increasing group size and food competition in folivores (Koenig 2002; Snaith and Chapman 2007). In the current study, group spread per individual increased as group size increased, however, no relationship was found between group spread and daily path length. Because the current analysis was limited to group means, variation often found for daily path lengths between seasons and even months is probably missing, confounding the overall relationship between daily path length and group spread. For example, Arrowood (2003) and colleagues found a significant correlation between group spread and daily path length in four groups of black howlers (*Alouatta pigra*), with daily path length increasing as group spread increased. This relationship became stronger when the amount of time spent feeding on leaves was incorporated into analyses, showing that groups spread out more, spent more time feeding on leaves, and visited more leafing trees on days they travelled more. Future studies ought to investigate how the percent of time feeding on preferred food items, such as immature leaves, fruits or flowers (Chapman and Chapman 2002; Koenig *et al.* 1998; Milton 1980; Oates 1994; Yeager and Kool 2000) affects group spread and/or ranging patterns in folivorous primates.

Folivores living in larger groups spent more time feeding and less time resting, however, these relationships were non-significant to Bonferroni corrected levels. If folivores require adequate time to digest fibrous foods (van Schaik 1983; Milton 1984; Janson and Goldsmith 1995, Lambert 2007), then reduced resting time is likely an important limiting factor for group size in folivores (Majola *et al.* 2008). Despite a positive relationship between daily path length and group size in folivores, no relationship was found between group size and time spent traveling. This relationship may be the product of larger groups traveling at a faster rate to visit more food trees. In fact, when comparing groups of red colobus, Gillespie and Chapman (2001) found that the larger group of 48 individuals traveled 36% more rapidly than the smaller group of 24 individuals. Moreover, greater rate of travel may be indicative of more goal directed travel, with some species traveling farther and faster when the potential rewards are greater (Milton 1980).

To test the hypothesis that immature leaves are a patchy resource, a likely cause of within-group feeding competition, group size and daily path length were compared to the percent of time groups spent feeding on immature leaves. Although a significant and positive relationship was found between group size and percent time feeding on immature leaves, there was no relationship between percent time feeding on immature leaves and daily path length. These conflicting results do not necessarily suggest that immature leaves are not patchy nor that within-group scramble competition is absent in folivores. Instead, increased time feeding with lower daily path lengths may indicate a greater level of between-group feeding competition. By monopolizing patchy leaf resources, larger groups would have less need to travel and thus spend more time foraging on immature leaves (or other preferred resources), procuring a serious fitness advantage over smaller groups. In observed between-group competition in red colobus (*Pilicolobus rufomitratus*), larger groups outcompeted smaller groups 80% of the time (Snaith and Chapman 2008).

Behavioral plasticity

Considerable variation in primate feeding habits exists not just within species, but within populations, and even within groups (Chapman and Rothman 2009). For example, Hanuman langurs have a highly flexible diet that varies from 19% to 86% leaves (Koenig and Borries 2001, 2002). The amount of time red colobus spend feeding on immature leaves in Kibale National Park, Uganda may differ as much as 38% (Chapman *et al.* 2002). Moreover, monthly temporal variation in the use of mature leaves for a single group of black-and-white colobus ranges from 5.9% to 91.6% (Harris and Chapman 2007).

Differences in diet may lead to variation in group size and the behavioral tactics utilized to alleviate within group feeding competition (Chapman and Rothman 2009; Koenig and Borries 2001; Saj and Sicotte 2007; Snaith and Chapman 2008). Such variable foraging strategies have been recorded for red colobus (Snaith and Chapman 2008). Of three large red colobus groups, one group fell in line with the ecological constraints model (Chapman and Chapman 2000; Janson 1988; Mason 1968; Milton

1984; Wrangham 2000) having a much longer daily path length than expected for their group size. A second group traveled relatively long distances when together, but also utilized a fissioning strategy, for which subgroups traveled much shorter distances (Snaith and Chapman 2008). Finally, the third group was reported to have rather short daily path lengths, but markedly increased group spread (Snaith and Chapman 2008). In addition, certain behavioral strategies may be more conducive to particular environments or habitats. 'High cost–high yield' strategies are more effective when habitat productivity is higher (Harrison 1985). Therefore, folivores inhabiting high quality areas may be more apt to utilize a 'high cost – high yield' strategy, resulting in longer daily path lengths than folivores living in low quality habitat. Recognizing that primates mitigate feeding competition in a variety of ways (i.e. creating subgroups or increasing group spread instead of increasing daily path length), creating sampling protocols that account for these alternative strategies may help researchers better define feeding competition in both frugivores and folivores.

CONCLUSION

With a number of previous studies unable to find a relationship between group size and daily path length in folivorous species (Clutton-Brock and Harvey 1977; Dias and Strier 2003; Fashing 2001; Janson and Goldsmith 1995; Struhsaker and Leland 1987; Yeager and Kool 2000), folivores have been designated as having little to no feeding competition (Isbell 1991; Isbell and Young 2002; Janson and Goldsmith 1995; Steenbeek and van Schaik 2001; Sterck *et al.* 1997; Wrangham 1980). However, daily path length is not the only behavioral indicator of within-group feeding competition. Groups may adjust activity budgets, group spread, and ranging patterns over time to compensate for larger group sizes (Snaith and Chapman 2007). Failure to make these adjustments would have greater costs for larger groups, resulting in lower rates of female fecundity (Dunbar 1988; van Schaik 1983, Whitten 1983). Researchers aiming to quantify feeding competition among primates must move beyond the use of single parameters like daily path length, and incorporate alternative behavioral indications of within-group competition such as increased group spread, changes in activity budgets, and decreased female fecundity (Saj

and Sicotte 2007, Koenig 2000). Presumably, finding a group size effect on at least one of these parameters (e.g. group spread) would indicate that feeding competition is occurring (Saj and Sicotte 2007). Also, more detailed comparisons of group dynamics and percent time spent feeding on preferred food items such as immature leaves and/or fruits are warranted to better understand how behavioral strategies are utilized among primate taxa (i.e, does subgrouping become more prevalent as the amount of fruit in the diet increases?). Furthermore, some behaviors may be responses to current ecological/social conditions while others may be constrained by evolutionary history. Comparative analyses of primate behavioral strategies should not be made without some investigation into the strength of phylogenetic relationships among the taxa being compared. Adopting the measures listed above will allow for better, more complete, comparisons across primate populations and taxa, an essential component of testing biological theory. The information gained from these future studies may finally lead to some resolution of the folivore paradox.

Table 1. Hypotheses and predictions (↑ represents an increase, ↓ represents a decrease).

Hypothesis	Independent Variable	Dependent Variable	Test(s)	Supported
Relative ranging cost constrains group size in frugivorous AND folivorous primates.	↑ Relative Ranging Cost	↓ Group size in frugivores ↓ Group size in folivores	OLS, PGLS, LMM	Yes No
Group size generates energetic and reproductive costs in frugivorous AND folivorous primates.	↑ Group Size	↑ Daily path length in frugivores ↑ Daily path length in folivores ↓ Infant:female ratio in frugivores ↓↓ Infant:female ratio in folivores	CCMM	Yes Yes Yes Yes
Folivorous primates utilize alternative strategies, in addition to increasing daily path length, to mediate within-group feeding competition.	↑ Folivore Group Size	↑ Group spread -If ↑ Group spread, ↓Daily path length ↑ Feeding ↑ Traveling ↓ Resting	LMM	Yes No Yes/No No No
Immature leaves are a patchy resource, thus, folivorous primates have daily path lengths that correlate to the amount of immature leaves in the diet.	↑ % Immature leaves in diet	↑ Daily path length	LMM	No

Tests: OLS = ordinary least squares regression; PGLS = phylogenetic generalized least squares regression; LMM = linear mixed effects model; CCMM = cross-classified mixed effects model.

Table 2. Variables used in cross-classified random effects models.

Variable Name	**Variable Type**	**Reason for Inclusion**
Annual Rainfall	Continuous	Proxy for habitat productivity
Diet	Categorical	Test differences between frugivores and folivores
Body Size	Continuous	Together with terrestriality serves as a proxy for risk of predation
Terrestriality	Categorical	Together with body size serves as a proxy for risk of predation
Female Dispersal	Categorical	Female philopatry may lead to different mechanisms of food competition where larger groups gain a foraging advantage (Wrangham 1980, Janson and Goldsmith 1995)
Infanticide	Categorical	Risk of infanticide may lead females to compete to keep groups small to avoid male take over (Crockett and Janson 2000)
Territoriality	Categorical	Ranging patterns of territorial animals may be more constrained by the need to monitor boundaries rather than feeding competition (Janson and Goldsmith 1995, but see Mitani and Rodman 1979)

Table 3. Regression results of daily path length (m) on primate group size. To calculate RRC the slope of the regression for each population is divided by the path length of a solitary individual [slope (m/ind) * 1 indiviudal + intercept (m)]. RRC provides an index of change in relative fitness due to the addition of one more group member (Janson and Goldsmith 1995). An inverse relationship is expected between RRC values and group size.

Species	Diet	Female Mass (Kg)	Arboreal	Female Dispersal	Territorial	Group Size			Intercept (m)	Slope (m/ind.)	r^2	RRC	References
						N	Mean	Max					
Eulemur fulvus rufus	F	2.25	A	F	N	2			421.0	57.5	---	0.12	Overdorff, 1991
Propithecus diadema	L	6.26	A	N	T	2	5.5	8	325.6	**114.0**	---	0.259	Wright, 1995
Propithecus edwardsii	F	5.86	A	N	T	2	5	6	268.0	108.5	---	0.288	Erhart & Overdorff, 2008
Propithecus verreauxi	L	2.95	A	N	T	2	5	6	1087.5	-68.8	---	-0.067	Richard, 1978
Callicebus moloch	F	0.96	A	F	T	3	3	4	248.8	106.3	0.741	0.299	Mason, 1968
Cebus apella	F	2.52	A	N	N	14	9.1	12	1171.5	70.1	0.281*	0.056	Janson 1988
Cebus olivaceus	F	2.52	A	N	N	2	15	23	2445.6	40.6	---	0.016	de Ruiter, 1986
Alouatta caraya	L	4.33	A	F	N	2	15	17	223.8	22.3	---	0.09	Bravo & Sallenave, 2003
Alouatta caraya	L	4.33	A	F	N	2	8	9	612.3	8.3	---	0.013	Kowalewski, 2007
Alouatta caraya	L	4.33	A	F	N	2	5.8	7.5	726.9	4.3	---	0.006	Agostini *et al.* 2010
Alouatta guariba	L	4.35	A	F	N	2	9.5	13	596.7	18.7	---	0.03	Agostini *et al.* 2010
Alouatta palliata	L	4.02	A	F	N	2	13.5	17	-245.2	48.6	---	---	Stoner, 1996
Alouatta palliata	L	6.45	A	F	N	2	13	16	317.3	0.7	---	0.002	Chivers, 1969
Alouatta palliata	L	6.45	A	F	N	4	15.7	23.4	-14.1	32.5	0.962*	---	Hopkins, 2008
Alouatta palliata	L	5.16	A	F	N	3	10.5	19	243.7	8.0	0.892	0.032	Larose, 1996
Alouatta pigra	L	6.43	A	F	N	4	5.5	8	321.8	22.8	0.559	0.066	Arrowood et al. 2003
Alouatta pigra	L	6.43	A	F	N	3	4	6	133.0	29.3	0.641	0.181	Knopff & Pavelka, 2006
Alouatta seniculus	L	4.67	A	F	N	4	9	10	468.8	-10.0	0.031	-0.022	Sekulic, 1982
Alouatta seniculus	L	6.3	A	F	N	2	5	6	523.5	0.8	---	0.002	Gomez-Posada *et al.* 2007
Alouatta seniculus	L	6.3	A	F	N	3	7.3	8	1036.9	-62.6	0.254	-0.064	Gomez-Posada *et al.* 2007
Ateles paniscus	F	8.44	A	F	N	22	3.6	8.8	728.0	359.3	0.546**	0.33	Symington, 1988
Lagothrix lagotricha	F	7.02	A	F	N	2	20	27	3196.4	-53.6	---	-0.017	Stevenson & Castellanos, 2000
Lagothrix lagotricha	F	7.02	A	F	N	2	19.8	26.5	1154.6	41.2	---	0.034	Stevenson, 2006

Table 3 (continued)

Lagothrix lagotricha	F	4.53	A	F	N	2	23.5	25	1790.0	4.0	---	0.002	Di Fiore, 2003
Cercopithecus ascanius	F	2.92	A	N	T	2	19.9	28.5	1627.2	-2.9	---	-0.002	Struhsaker & Leland, 1988
Cercopithecus diana	F	3.9	A	N	T	2	18.5	23	250.6	54.9	---	0.18	Whitesides, 1989
Cercopithecus mitis	F	3.93	A	N	T	4	15.6	22	1450.4	-14.7	0.778	-0.01	Butynski, 1990
Cercopithecus aethiops	F	2.98	T	N	T	2	11.5	19	33.5	2.6	---	0.072	Isbell *et al*. 1998
Erythrocebus patas	F	6.5	T	N	N	2	24	35	3599.6	17.7	---	0.005	Chism & Rowell, 1988
Chlorocebus djamdjamensis	L	2.98	A	N	---	2	53	58	619.6	5.8	---	0.009	Mekennon *et al.* 2010
Lophocebus albigena	F	6.02	A	N	N	4	16.3	28	492.7	50.8	0.94*	0.093	Waser, 1977
Macaca fascicularis	F	3.59	A	N	N	5	21.6	31	924.6	20.3	0.569	0.022	van Schaik et al., 1983
Macaca nigra	F	5.47	T	N	N	3	60.7	84.5	957.5	23.6	0.547	0.024	O'Brien & Kinnaird, 1997
Papio ursinus	F	14.8	T	N	N	59	39	82	1588.7	36.3	0.5**	0.023	Anderson, 1980
Rungwecebus kipinji	L	13	A	N	N	4	38.8	50	1766.5	-12.2	0.113	-0.007	de Luca *et al*. 2009
Colobus guareza	L	9.2	A	N	T	5	10.6	19	464.1	10.2	0.291	0.021	Fashing, 2001
Colobus guareza	L	9.2	A	N	T	2	6	8	312.0	-1.8	---	-0.006	Harris *et al.* 2009
Colobus satanas	L	7.42	A	N	N	2	14.3	17.5	195.1	37.5	---	0.161	Fleury & Gautier-Hion, 1999
Colobus vellerosus	L	6.9	A	N	N	2	15	23	218.4	6.0	---	0.027	Saj & Sicotte, 2007
Colobus vellerosus	L	6.9	A	N	N	2	18.5	23	416.5	-7.5	---	-0.018	Saj & Sicotte, 2007
Colobus vellerosus	L	6.9	A	N	N	5	15.8	25	280.7	5.0	0.508	0.017	Teichrob, 2009
Piliocolobus rufomitratus	L	7.21	A	F	N	9	65.2	127	471.2	1.5	0.08	0.003	Snaith and Chapman, 2008
Piliocolobus tephrosceles	L	8.21	A	F	N	3	20.3	32	927.7	-12.7	0.984	-0.014	Struhsaker, 2010
Piliocolobus tephrosceles	L	8.21	A	F	N	3	27.6	47.6	573.7	-0.2	0.069	0	Struhsaker, 2010
Piliocolobus tephrosceles	L	8.21	A	F	N	2	36	48	41.0	11.2	---	0.214	Gillespie & Chapman, 2001
Piliocolobus kirkii	L	5.46	A	N	N	3	28	33	710.6	-5.2	0.448	-0.007	Siex, 2003
Procolobus kirkii	L	5.46	A	N	N	4	31.3	54	264.1	1.5	0.517	0.006	Siex, 2003
Presbytis thomasi	L	6.69	A	F	N	14	6.7	11	665.9	60.2	0.594**	0.083	Steenbeek & van Schaik, 2001

Table 3 (continued)

Semnopithecus entellus	L	14.8	T	F	T	2	19	22.5	448.9	19.3	---	0.041	Schlicting, 2008
Gorilla beringei	L	97.5	T	F	N	6	13.7	18	277.6	13.5	0.121	0.046	Schaller, 1963
Gorilla beringei	L	97.5	T	F	N	4	7.5	12	376.3	30.3	0.974*	0.075	Watts, 1991
Gorilla beringei	L	97.5	T	F	N	2	9.5	11	100.2	40.9	---	0.29	Fossey & Harcourt, 1977
Gorilla beringei	L	97.5	T	F	N	11	9.2	15	151.4	15.7	0.497*	0.094	Goldsmith, 1993
Gorilla beringei	L	97.5	T	F	N	4	14.8	24	475.7	18.7	0.495	0.038	Ganas & Robbins 2005
Pan troglodytes verus	F	41.6	T	F	T	3	21.7	36	1624.0	72.9	0.992	0.043	Herbinger *et al.*, 2001
Symphalangus syndactylus	F	10.7	A	F	T	2	2.3	3	763.5	108.7	---	0.125	Chivers *et al.* 1975

Probability levels for regressions are two-tailed and test the null hypothesis that the slopes are equal to zero (* = < 0.05, ** = < 0.01).

Diet: F = Frugivore, L = Leaf-eating; Arboreal: A = Arboreal, T = Terrestrial; Female Dispersal: F = Female dispersal, N = No female dispersal

Territorial: T = Territorial, N= Not territorial; Group Size: N = Number of groups studies.

Table 4. Results of linear mixed effects model (LMM) testing the relationship between RRC, diet, and group size. Species nested within genus, nested within family, was set as a random factor to alleviate taxonomic clustering of closely related taxa. The model was fit by ML (n=54 observations).

Response Variable	Fixed Effects	Coefficient (Estimate)	Standard Error	t-value	p-value
log (Ave Group Size)	(Intercept)	1.343	0.088	15.271	<0.001
	RRC	-2.511	0.631	-3.982	<0.001
	Diet (Leaves)	-0.210	0.112	-1.865	0.068
	RRC:Diet (Leaves)	2.404	0.740	3.248	0.002

81% Variance explained by the nested random factor Species/Genus/Family

Table 5. Results of cross-classified random effects model (CCMM) testing the relationship between group size, diet, and daily path length. To account for the cross-cutting hierarchical structure of the data (study population and taxonomy), study population and species nested within genus, nested within family were set as crossed random factors. The model was fit by ML (n = 197 observations).

Response Variable	Fixed Effects	Coefficient (Estimate)	Standard Error	t-value	p-value
DPL	(Intercept)	6.382	0.165	38.59	<0.001
	log (Group Size)	0.396	0.054	7.39	<0.001
	Diet (Leaves)	-0.515	0.226	-2.27	0.024
	log (Group Size):Diet (Leaves)	-0.201	0.073	-2.76	0.006

25.7% Variance explained by study
49.5% Variance explained by Species/Genus/Family

Table 6. Results of cross-classified random effects model (CCMM) testing the relationship between group size and female fecundity (ratio of infants to adult females). Study population and species nested within genus, nested within family were set as crossed random factors to alleviate the cross-cutting hierarchical structure of the data (study population and taxonomy). The model was fit by ML (n=90 observations).

Response Variable	**Fixed Effects**	**Coefficient (Estimate)**	**Standard Error**	**t-value**	**p-value**
Infant:Female	(Intercept)	1.168	0.355	3.292	0.002
	log (Group Size)	-0.431	0.113	-3.808	<0.001
	Diet (Leaves)	-0.118	0.382	-0.331	0.742
	log (Adult Female Body Mass)	0.041	0.153	0.268	0.789
	Terrestriality	2.225	3.411	6.523	<0.001
	Female Dispersal	0.779	0.196	3.981	<0.001
	Annual Rainfall (mm)	0	0	-2.499	0.015
	log (Group Size):Diet (Leaves)	0.298	0.128	2.328	0.023
	log (Adult Female Body Mass): Terrestriality	-0.491	0.150	-3.284	0.002
	Diet (Leaves):Female Dispersal	-0.766	0.221	-3.475	<0.001

0% Variance explained by study

0% Variance explained by Species/Genus/Family

Table 7. Results of cross-classified random effects model (CCMM) testing the relationship between presence of infanticide within a species and diet on group size. To account for the cross-cutting hierarchical structure of the data (study population and taxonomy), study population and species nested within genus, nested within family were set as crossed random factors. The model was fit by ML (n = 187 observations).

Response Variable	**Fixed Effects**	**Coefficient (Estimate)**	**Standard Error**	**t-value**	**p-value**
log (Ave Group Size)	(Intercept)	2.45	0.317	7.714	<0.001
	Infanticide	-0.063	0.401	-0.158	0.443
	Diet (Leaves)	0.556	0.629	0.884	0.928
	Infanticide:Diet (Leaves)	-0.590	0.706	-0.835	0.405

3.08% Variance explained by study
67.5% Variance explained by Species/Genus/Family

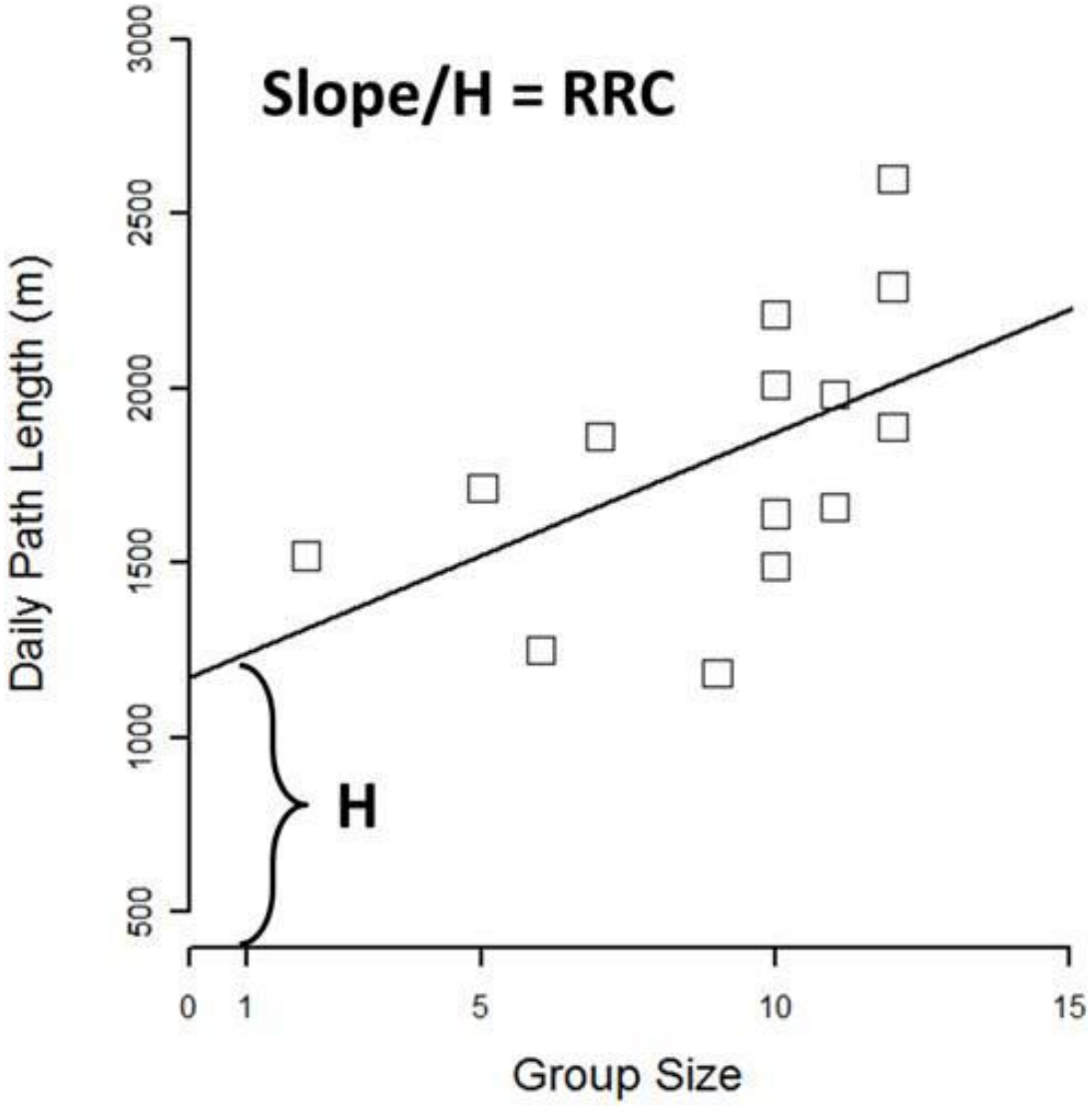

Figure 1. Calculation of relative ranging cost (RRC). RRC measures the increased ranging cost of an additional group member by dividing the slope (S) of the regression relating daily path length to group size by the daily path length at group size of 1 (H). Data are from Cebus apella (Janson 1988). These data deviate significantly from a linear regression ($y = 74.1x + 1117.4$, $r2 = 0.281$, $N = 14$, $p < 0.05$).

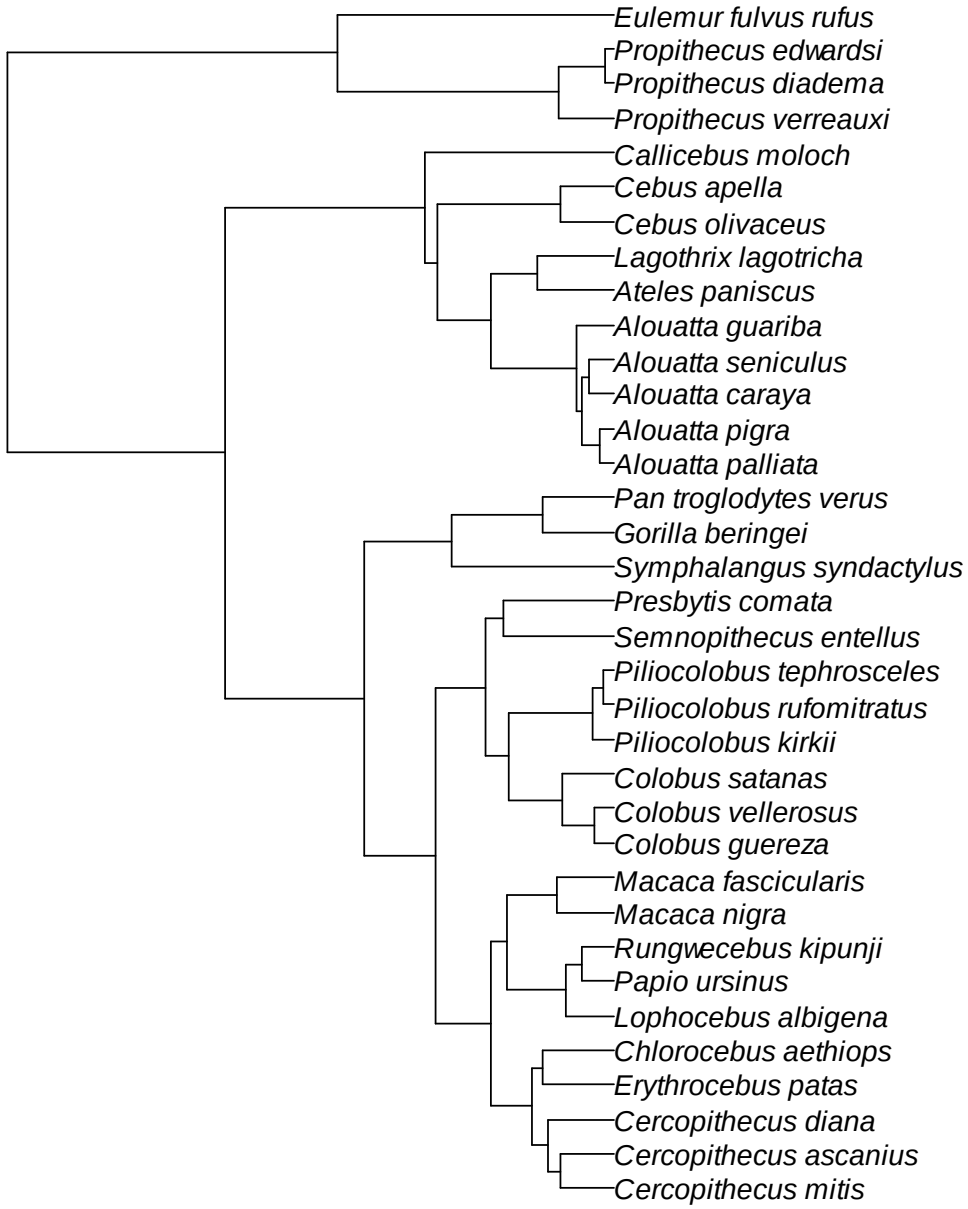

Figure 2. 10K consensus tree used for phylogenetic generalized least squares regression (PGLS) analyses. When creating this tree *Presbytis comata* was substituted for *P. thomasi.* This had no effect on phylogenetic relationships within the tree since these taxa have the same divergence time from *Semnopithecus entellus* (Meyer 2011). Phylogenetic relationships have not been confirmed for *Chlorocebus djamdjamensis*, therefore, this taxon was left out of PGLS analyses.

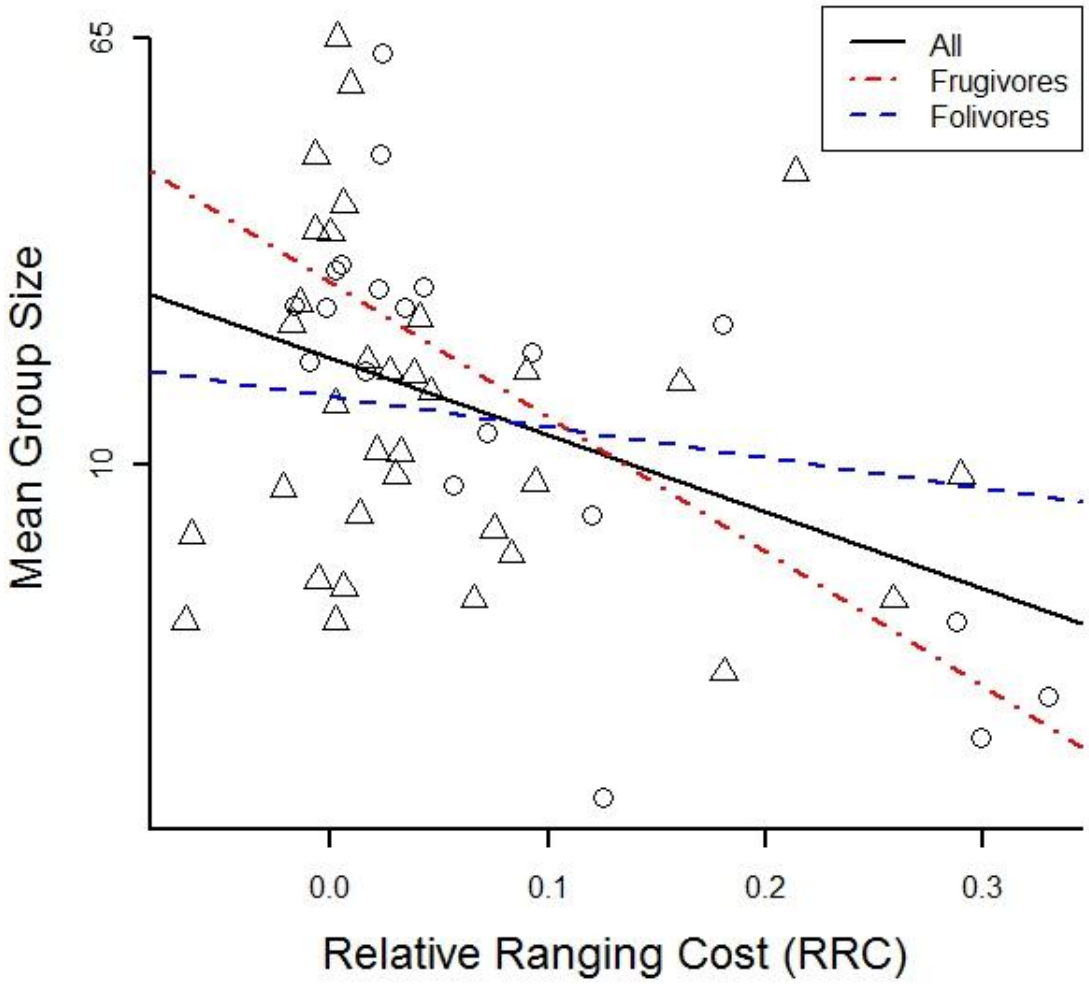

Figure 3. The relationship between mean observed groups size and relative ranging cost. Frugivores are represented by circles and the regression by a dashed red line ($\log_{10}(y) = 1.346 - 2.565x$, $r^2 = 0.536$, $n = 18$, $p < 0.001$). Folivores are represented by triangles and the regression by a dashed blue line ($\log_{10}(y) = 1.129 - 0.586x$, $r^2 = 0.025$, $n = 32$, $p > 0.374$). The regression line for all groups is represented by a solid black line ($\log_{10}(y) = 1.2 – 1.46x$, $r^2 = 0.174$, $n = 52$, $p < 0.01$).

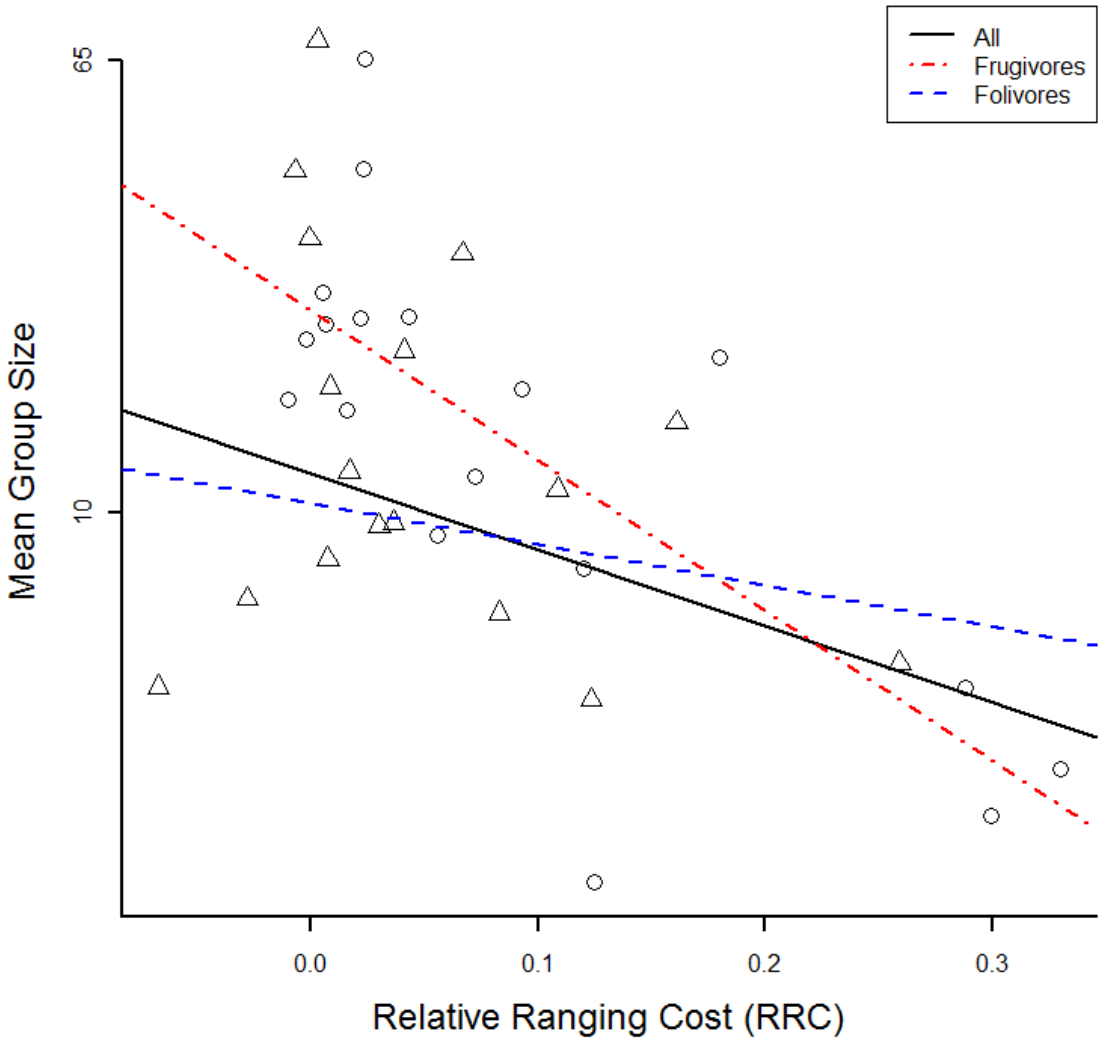

Figure 4. The relationship between mean observed groups size and relative ranging cost while controlling for phylogeny. Frugivores are represented by circles and the regression by a dashed red line ($\ln(y) = 3.1 - 5.956x$, $r^2 = 0.553$, $n = 18$, $p < 0.001$). Folivores are represented by triangles and the regression by a dashed blue line ($\ln(y) = 2 - 1.63x$, $r^2 = 0.061$, $n = 17$, $p = 0.397$). The regression line for all species is represented by a solid black line ($\ln(y) = 2.46 - 3.03x$, $r^2 = 0.218$, $n = 35$, $p < 0.001$).

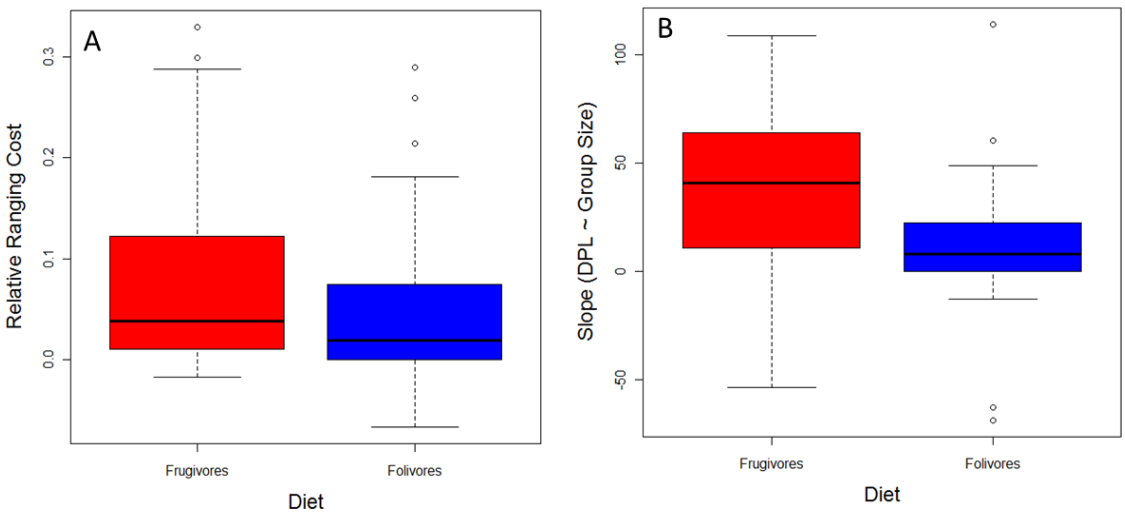

Figure 5. Boxplots of relative ranging cost (A) and slope (B) by diet type. RRC values were not significantly different between frugivores and folivores (WRST, W = 419, p = 0.160). Slope values, however, were significantly different between the two diet types (WRST, W=449, $p < 0.01$).

Appendix I. Daily path length and behavioral data used in analyses.

Study Index	Species	Diet	Group Size	Daily Path Length (m)	Infant:female ratio	Annual Rainfall (mm)	Female Mass (Kg)	Female Dispersal	Arboreal	Territorial	Infanticide	DPL Source and Behavior Source Exceptions
1	Eulemur fulvus rufus	F	9	938.5	---	2300	2.25	F	A	N	I	Overdorff, 1991
	Eulemur fulvus rufus	F	7	823.5	---	2300	2.25	F	A	N	I	
2	Propithecus diadema	L	3	667.6	---	2300	6.26	N	A	T	I	Wright, 1995
	Propithecus diadema	L	8	1237.6	---	2300	6.26	N	A	T	I	
3	Propithecus edwardsii	F	6	919	0	2300	5.86	N	A	T	I	Erhart and Overdorff, 1991; infanticide: Erhart & Overdorff, 1998
	Propithecus edwardsii	F	4	702	0	2300	5.86	N	A	T	I	
4	Propithecus verreauxi	L	6	675	1	630	2.95	N	A	T	I	Richard, 1978
	Propithecus verreauxi	L	4	812.5	0.5	630	2.95	N	A	T	I	
5	Callicebus moloch	F	2	425	---	1400	0.96	F	A	T	N	Mason, 1968
	Callicebus moloch	F	4	637.5	---	1400	0.96	F	A	T	N	
	Callicebus moloch	F	3	640	---	1400	0.96	F	A	T	N	
6	Cebus apella	F	2	1520	---	2000	2.52	N	A	N	I	Janson, 1988
	Cebus apella	F	5	1715	---	2000	2.52	N	A	N	I	
	Cebus apella	F	6	1250	---	2000	2.52	N	A	N	I	
	Cebus apella	F	7	1860	---	2000	2.52	N	A	N	I	
	Cebus apella	F	9	1185	---	2000	2.52	N	A	N	I	
	Cebus apella	F	10	1490	---	2000	2.52	N	A	N	I	
	Cebus apella	F	10	1640	---	2000	2.52	N	A	N	I	
	Cebus apella	F	10	2010	---	2000	2.52	N	A	N	I	

	Cebus apella	F	10	2210	---	2000	2.52	N	A	N	I	
	Cebus apella	F	11	1660	---	2000	2.52	N	A	N	I	
	Cebus apella	F	11	1980	---	2000	2.52	N	A	N	I	
	Cebus apella	F	12	1890	---	2000	2.52	N	A	N	I	
	Cebus apella	F	12	2290	---	2000	2.52	N	A	N	I	
	Cebus apella	F	12	2600	---	2000	2.52	N	A	N	I	
7	Cebus olivaceus	F	23	3380	0.22	1480	2.52	N	A	N	I	De Ruiter, 1986
	Cebus olivaceus	F	7	2730	0.33	1480	2.52	N	A	N	I	
8	Alouatta caraya	L	13	513	0.6	1230	4.33	F	A	N	I	Bravo & Sallenave, 2003
	Alouatta caraya	L	17	602	0.67	1230	4.33	F	A	N	I	
9	Alouatta caraya	L	9	686.5	0.5	1230	4.33	F	A	N	I	Kowalewski, 2007
	Alouatta caraya	L	7	670	0.67	1230	4.33	F	A	N	I	
10	Alouatta caraya	L	7.5	759	0.33	1952	4.33	F	A	N	I	Agostini *et al.* 2010
	Alouatta caraya	L	4	744	0.83	1952	4.33	F	A	N	I	
11	Alouatta guariba	L	13	840	0.4	1952	4.35	F	A	N	---	
	Alouatta guariba	L	6	709	0.5	1952	4.35	F	A	N	---	
12	Alouatta palliata	L	17	581.2	0.2	3962	4.02	F	A	N	I	Stoner, 1996
	Alouatta palliata	L	10	240.9	0.2	3962	4.02	F	A	N	I	
13	Alouatta palliata	L	10	324	0.4	2500	6.45	F	A	N	I	Chivers, 1969; female mass: Glander, 2006
	Alouatta palliata	L	16	328	0.4	2500	6.45	F	A	N	I	
14	Alouatta palliata	L	13.6	453	---	2500	6.45	F	A	N	I	Hopkins 2008; female mass: Glander, 2006
	Alouatta palliata	L	23.4	770	---	2500	6.45	F	A	N	I	
	Alouatta palliata	L	16.8	474	---	2500	6.45	F	A	N	I	
	Alouatta palliata	L	9	288	---	2500	6.45	F	A	N	I	
15	Alouatta palliata	L	4.5	262	0.71	1473	5.16	F	A	N	I	LaRose, 1996; female mass: Glander, 2006
	Alouatta palliata	L	8	331	0.79	1473	5.16	F	A	N	I	
	Alouatta palliata	L	19	390	0.46	1473	5.16	F	A	N	I	
16	Alouatta pigra	L	3	354	---	1500	6.43	F	A	N	I	Arrowood *et al.* 2003

	Alouatta pigra	L	5	494	---	1500	6.43	F	A	N	I	
	Alouatta pigra	L	6	462	---	1500	6.43	F	A	N	I	
	Alouatta pigra	L	8	479	---	1500	6.43	F	A	N	I	
17	Alouatta pigra	L	3	183	0	2500	6.43	F	A	N	I	Knopff & Pavelka, 2006; infanticide: Knopff *et al.* 2004
	Alouatta pigra	L	3	259	0.5	2500	6.43	F	A	N	I	
	Alouatta pigra	L	6	309	0.5	2500	6.43	F	A	N	I	
18	Alouatta seniculus	L	8	375	0.67	1585	4.67	F	A	N	I	Sekulic, 1982
	Alouatta seniculus	L	10	355	0.5	1585	4.67	F	A	N	I	
	Alouatta seniculus	L	9	340	0.5	1585	4.67	F	A	N	I	
	Alouatta seniculus	L	9	445	0.67	1585	4.67	F	A	N	I	
19	Alouatta seniculus	L	4	526.7	0.5	2118	6.3	F	A	N	I	Gomez-Posada *et al.* 2007
	Alouatta seniculus	L	6	528.3	1	2118	6.3	F	A	N	I	
20	Alouatta seniculus	L	8	412.2	0.67	2118	6.3	F	A	N	I	Gomez-Posada *et al.* 2007
	Alouatta seniculus	L	6	661.3	1	2118	6.3	F	A	N	I	
	Alouatta seniculus	L	8	660	1	2118	6.3	F	A	N	I	
21	Ateles paniscus	F	1.7	1020	---	2000	8.44	F	A	N	I	Symington, 1988; infanticide: Gibson *et al.* 2008
	Ateles paniscus	F	1.8	1465	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.1	835	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.2	1095	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.3	1920	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.3	1080	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.4	515	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.4	1990	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.5	1830	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	2.8	2545	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	3	1905	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	3.1	2580	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	3.5	1620	---	2000	8.44	F	A	N	I	

	Ateles paniscus	F	4.2	1915	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	4.2	2335	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	4.5	3085	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	4.8	3045	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	5.1	2000	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	5.2	2505	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	5.6	2505	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	5.5	3745	---	2000	8.44	F	A	N	I	
	Ateles paniscus	F	8.8	3225	---	2000	8.44	F	A	N	I	
22	Lagothrix lagotricha	F	13	2500	0.2	2622	7.02	F	A	N	N	Stevenson & Castellanos, 2000
	Lagothrix lagotricha	F	27	1750	0.2	2622	7.02	F	A	N	N	
23	Lagothrix lagotricha	F	26.5	2246	0.38	2782	7.02	F	A	N	N	Stevenson, 2006
	Lagothrix lagotricha	F	13	1690	0.44	2782	7.02	F	A	N	N	
24	Lagothrix lagotricha	F	25	1890	0	3276	4.53	F	A	N	N	Di Fiore, 2003
	Lagothrix lagotricha	F	22	1878	0	3276	4.53	F	A	N	N	
25	Cercopithecus ascanius	F	28.5	1546	---	1490	2.92	N	A	T	I	Struhsaker & Leland, 1988
	Cercopithecus ascanius	F	11.3	1595	---	1490	2.92	N	A	T	I	
26	Cercopithecus diana	F	14	1019	---	3000	3.9	N	A	T	---	Whitesides, 1989
	Cercopithecus diana	F	23	1513	---	3000	3.9	N	A	T	---	
27	Cercopithecus mitis	F	14.5	1300	---	1570	3.93	N	A	T	I	Butynski, 1990
	Cercopithecus mitis	F	9	1291	---	1570	3.93	N	A	T	I	
	Cercopithecus mitis	F	22	1115	---	1570	3.93	N	A	T	I	
	Cercopithecus mitis	F	17	1176	---	1570	3.93	N	A	T	I	
28	Chlorocebus aethiops	F	4	43.8	3	600	2.98	N	T	T	I	Isbell *et al.* 1998
	Chlorocebus aethiops	F	19	82.6	1.22	600	2.98	N	T	T	I	
29	Erythrocebus patas	F	13	3830	0.75	630	6.5	N	T	N	I	Chism & Rowell, 1988; infanticide: Enstam *et al.* 2002
	Erythrocebus patas	F	35	4220	0.75	630	6.5	N	T	N	I	
30	Chlorocebus djamdjamensis	L	58	956	---	796	2.98	---	A	---	---	Mekennon *et al.* 2010

	Chlorocebus djamdjamensis	L	48	898	---	796	2.98	---	A	---	---	
31	Lophocebus albigena	F	6	910	---	1658	6.02	N	A	N	N	Waser, 1977
	Lophocebus albigena	F	15	1160	---	1658	6.02	N	A	N	N	
	Lophocebus albigena	F	16	1200	---	1658	6.02	N	A	N	N	
	Lophocebus albigena	F	28	2000	---	1658	6.02	N	A	N	N	
32	Macaca fascicularis	F	10	1350	---	3229	3.59	N	A	N	I	Van Schaik *et al.* 1983
	Macaca fascicularis	F	11	900	---	3229	3.59	N	A	N	I	
	Macaca fascicularis	F	26.5	1500	---	3229	3.59	N	A	N	I	
	Macaca fascicularis	F	29.5	1620	---	3229	3.59	N	A	N	I	
	Macaca fascicularis	F	31	1450	---	3229	3.59	N	A	N	I	
33	Macaca nigra	F	84.5	3140	---	1760	5.47	N	T	N	N	O'Brien & Kinnaird, 1997
	Macaca nigra	F	56.5	1750	---	1760	5.47	N	T	N	N	
	Macaca nigra	F	41	2270	---	1760	5.47	N	T	N	N	
34	Rungwecebus kipunji	L	32	1204	---	2186	13	N	A	N	---	De Luca *et al.* 1997; female mass: Erhardt *et al.* 2006
	Rungwecebus kipunji	L	40	995	---	2186	13	N	A	N	---	
	Rungwecebus kipunji	L	50	1262.5	---	2186	13	N	A	N	---	
	Rungwecebus kipunji	L	33	1712	---	2186	13	N	A	N	---	
35	Colobus guareza	L	9	434	0.4	2215	9.2	N	A	T	I	Fashing, 2001
	Colobus guareza	L	5	614	0.67	2215	9.2	N	A	T	I	
	Colobus guareza	L	8	552	1	2215	9.2	N	A	T	I	
	Colobus guareza	L	12	551	0.75	2215	9.2	N	A	T	I	
	Colobus guareza	L	19	708	0.5	2215	9.2	N	A	T	I	
36	Colobus guareza	L	8	298	0.33	1570	9.2	N	A	T	I	Harris *et al.* 2010
	Colobus guareza	L	4	305	1	1570	9.2	N	A	T	I	
37	Colobus satanas	L	17.5	852	---	1721	7.42	N	A	N	N	Fleury & Gautier-Hion, 1999
	Colobus satanas	L	11	608	---	1721	7.42	N	A	N	N	
38	Colobus vellerosus	L	23	357	0.73	984	6.9	N	A	N	I	Saj & Sicotte, 2007
	Colobus vellerosus	L	7	260.6	0.33	984	6.9	N	A	N	I	

39	Colobus vellerosus	L	23	243.5	0.73	984	6.9	N	A	N	I	Saj & Sicotte, 2007
	Colobus vellerosus	L	14	311.2	0.33	984	6.9	N	A	N	I	
40	Colobus vellerosus	L	7	331	1	1329	6.9	N	A	N	I	Teichrob, 2009
	Colobus vellerosus	L	9.5	336	1.13	1329	6.9	N	A	N	I	
	Colobus vellerosus	L	16.5	336	0.5	1329	6.9	N	A	N	I	
	Colobus vellerosus	L	21	339	0.47	1329	6.9	N	A	N	I	
	Colobus vellerosus	L	25	453	0.33	1329	6.9	N	A	N	I	
41	Piliocolobus rufomitratus	L	70	507	---	1570	7.21	F	A	N	I	Snaith & Chapman, 2008
	Piliocolobus rufomitratus	L	25	475	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	84	640	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	45	520	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	127	520	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	51	510	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	40	425	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	74	950	---	1570	7.21	F	A	N	I	
	Piliocolobus rufomitratus	L	71	555	---	1570	7.21	F	A	N	I	
42	Piliocolobus tephrosceles	L	20	653	---	1570	8.21	F	A	N	I	Struhsaker, 2010
	Piliocolobus tephrosceles	L	32	533	---	1570	8.21	F	A	N	I	
	Piliocolobus tephrosceles	L	9	825	---	1570	8.21	F	A	N	I	
43	Piliocolobus tephrosceles	L	47.6	570	---	1490	8.21	F	A	N	I	Struhsaker, 2010
	Piliocolobus tephrosceles	L	24.8	551	---	1490	8.21	F	A	N	I	
	Piliocolobus tephrosceles	L	10.3	582	---	1490	8.21	F	A	N	I	
44	Piliocolobus tephrosceles	L	48	577	---	1778	8.21	F	A	N	I	Gillespie & Chapman, 2001
	Piliocolobus tephrosceles	L	24	309	---	1778	8.21	F	A	N	I	
45	Piliocolobus kirkii	L	31	506.5	0.23	1600	5.46	N	A	N	N	Siex, 2003
	Piliocolobus kirkii	L	33	576	0.23	1600	5.46	N	A	N	N	
	Piliocolobus kirkii	L	20	613.5	0.3	1600	5.46	N	A	N	N	
46	Piliocolobus kirkii	L	16	309.5	0.56	1600	5.46	N	A	N	N	Siex, 2003

	Piliocolobus kirkii	L	54	358	0.48	1600	5.46	N	A	N	N	
	Piliocolobus kirkii	L	32	280	0.35	1600	5.46	N	A	N	N	
	Piliocolobus kirkii	L	23	293.75	0.36	1600	5.46	N	A	N	N	
47	Presbytis thomasi	L	8	1066	---	3229	6.69	F	A	N	I	Steenbeek & van Schaik, 2001
	Presbytis thomasi	L	7	1193	1	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	9	1264	1	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	5	1078	0	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	7	1228	1	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	6	948	0	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	6	1049	0	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	11	1189	0.25	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	7	1094	0	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	7	1170	---	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	7	1143	0.5	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	5	903	---	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	3	754	1	3229	6.69	F	A	N	I	
	Presbytis thomasi	L	5.5	869	0.33	3229	6.69	F	A	N	I	
48	Semnopithecus entellus	L	15.4	746	---	2092	14.8	F	T	T	I	Schlicting, 2008
	Semnopithecus entellus	L	22.5	883	---	2092	14.8	F	T	T	I	
49	Gorilla beringei	L	11	547	0.17	1924	97.5	F	T	N	I	Ganas & Robbins, 2005
	Gorilla beringei	L	24	847	0.46	1924	97.5	F	T	N	I	
	Gorilla beringei	L	17	978	0.63	1924	97.5	F	T	N	I	
	Gorilla beringei	L	7	633	0.2	1924	97.5	F	T	N	I	
50	Gorilla beringei	L	15	495.3	0.67	1811	97.5	F	T	N	I	Schaller, 1963
	Gorilla beringei	L	18	473.4	0.6	1811	97.5	F	T	N	I	
	Gorilla beringei	L	9	337.1	0.67	1811	97.5	F	T	N	I	
	Gorilla beringei	L	13	378.6	0.78	1811	97.5	F	T	N	I	
	Gorilla beringei	L	13	663.5	0.83	1811	97.5	F	T	N	I	

	Gorilla beringei	L	14	426.7	0.88	1811	97.5	F	T	N	I	
51	Gorilla beringei	L	2	445	---	1811	97.5	F	T	N	I	Watts, 1991
	Gorilla beringei	L	7	590	---	1811	97.5	F	T	N	I	
	Gorilla beringei	L	9	620	---	1811	97.5	F	T	N	I	
	Gorilla beringei	L	12	760	---	1811	97.5	F	T	N	I	
52	Gorilla beringei	L	11	450	---	1811	97.5	F	T	N	I	Fossey & Harcourt, 1977
	Gorilla beringei	L	8	350	---	1811	97.5	F	T	N	I	
53	Pan troglodytes verus	F	22	3340	1.08	1800	41.6	F	T	T	I	Herbinger *et al.* 2007
	Pan troglodytes verus	F	7	2080	1.33	1800	41.6	F	T	T	I	
	Pan troglodytes verus	F	36	4190	1.17	1800	41.6	F	T	T	I	
54	Symphalangus syndactylus	F	3	1089.5	0.5	2000	10.7	F	A	T	N	Chivers, 1969
	Symphalangus syndactylus	F	1.5	926.5	---	2000	10.7	F	A	T	N	

For each population, demographic, diet, habitat, and ranging data came from the DPL Source listed. Unless otherwise noted, the remaining data were drawn from the following sources: adult female mass (Smith & Jungers, 1997); arboreality (Schmitt, 2010); infanticide (van Noordwijk & van Schaik, 2000); female dispersal and territoriality (Campbell *et al.* 2011).

Diet: F = Frugivore, L = Leaf-eating

Female Dispersal: F = Female dispersal, N = No female dispersal

Arboreal: A = Arboreal, T = Terrestrial

Territorial: T = Territorial, N= Not territorial

Infanticide: I = Infanticide reported in species, N = No infanticide reported in species

Appendix II. Data used for group spread, activity budget, and diet analyses.

Study Index	Species	Group Size	Daily Path Length (m)	Group Spread (m)	% Rest	% Feed	% Travel	% Mature Leaves	% Immature Leaves	% Fruit	Source
4	Propithecus verreauxi	6	675			42.7					Richard, 1978
	Propithecus verreauxi	4	812.5			48.1					
9	Alouatta caraya	9	686.5	49.2	61.56	14.89	17.68	4	37	27	Kowalewski, 2007
	Alouatta caraya	7	670	51.7	55.73	16.14	20.27	9	44	22	
12	Alouatta palliata	17	581.2		53	24	18	6	65	17	Stoner, 1996
	Alouatta palliata	10	240.9		59	25.5	10	2	62	29	
13	Alouatta palliata	10	324		54	23	11				Chivers, 1969
	Alouatta palliata	16	328		57	25	7				
14	Alouatta palliata	13.6	453			15.1			37		Hopkins, 2008
	Alouatta palliata	23.4	770			11.6			38		
15	Alouatta palliata	4.5	262					31.5	30.5	18	LaRose, 1996
	Alouatta palliata	8	331					28	35	15.5	
	Alouatta palliata	19	390					20.9	37.3	15	
16	Alouatta pigra	3	354	6							Arrowood *et al.* 2003
	Alouatta pigra	5	494	9							
	Alouatta pigra	6	462	20							
	Alouatta pigra	8	479	20							
17	Alouatta pigra	3	183		82	15					Knopff & Pavelka, 2006
	Alouatta pigra	3	259		81	14					
	Alouatta pigra	6	309		84	11.5					
35	Colobus guareza	9	434		63.2	28.3	1.8	4.6	24.2	42.6	Fashing, 2001
	Colobus guareza	5	614		63.5	22.9	2.8	8.6	23.2	32.1	

38	Colobus vellerosus	23	357	65.5		28.9					Saj & Sicotte, 2007
	Colobus vellerosus	7	260.6	28		26.9					
39	Colobus vellerosus	23	243.5	65.5		33.6					Saj & Sicotte, 2007
	Colobus vellerosus	14	311.2	33.5		22.9					
40	Colobus vellerosus	7	331	33	76.5	19.5	1.2	36.3	35.1	11.6	Teichrob, 2009
	Colobus vellerosus	9.5	336	49	76.4	20.4	1.2	31.7	47.2	5.1	
	Colobus vellerosus	16.5	336	49	77.6	19.7	1.4	31.1	50	6.1	
	Colobus vellerosus	21	339	54	72.5	23.8	1	55.5	26.5	0.8	
	Colobus vellerosus	25	453	62	71.1	26	1.5	25.9	53	2.1	
41	Piliocolobus rufomitratus	70	507	46.5							Snaith & Chapman, 2008
	Piliocolobus rufomitratus	25	475	27.6							
	Piliocolobus rufomitratus	84	640	68.6							
	Piliocolobus rufomitratus	45	520	24.5							
	Piliocolobus rufomitratus	127	520	132.55							
	Piliocolobus rufomitratus	51	510	55.3							
	Piliocolobus rufomitratus	40	425	25.2							
	Piliocolobus rufomitratus	74	950	66.8							
	Piliocolobus rufomitratus	71	555	52.3							
44	Piliocolobus tephrosceles	48	577	66.14							Gillespie & Chapman, 2001
	Piliocolobus tephrosceles	24	309	51.67							
45	Piliocolobus kirkii	31	506.5		47.52	29.7	11.46	0.1	63.38	20.26	Siex, 2003
	Piliocolobus kirkii	33	576		48.3	29.28	11.05	1.94	52.16	20.94	
	Piliocolobus kirkii	20	613.5		45.93	27.14	13.92	0.87	36.52	29.86	
46	Piliocolobus kirkii	16	309.5		48.45	24.84	5.92	0.22	53.75	10.75	Siex, 2003
	Piliocolobus kirkii	54	358		39.16	30.52	6.27	0.94	60.73	2.59	
	Piliocolobus kirkii	32	280		45.1	27.39	5.95	0.85	56.62	1.51	
	Piliocolobus kirkii	23	293.75		42.67	31.76	5.68	0.85	56.62	1.51	

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Vita

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